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Characterizing the litter in postfire environments: implications for seedling recruitment

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Characterizing the litter in postfire environments: implications for seedling recruitment

Abstract

Litter accumulation after fire influences the magnitude of seed predation and seed germination. How litter accumulation and patchiness influence postfire seedling recruitment is poorly known. Species with persistent seed banks have seeds available for germination in the immediate postfire period. In contrast, plants with transient seed banks must flower after fire to place seeds in the postfire habitat. In southeastern Australian sclerophyll forests, most seedling recruitment occurs within 3 yr after fire. We found that less litter had accumulated in sites mass, including some species with very light seeds. In contrast, the seed mass of transient seed bank species is less variable, with the lightest species more than 70 times heavier than the lightest persistent seed bank species. These seeds arrive 1-3 yr postfire and encounter habitats with more litter and fewer bare patches. This pattern suggests that litter accumulation after fire has influenced the evolution of seed mass either directly, by affecting germination and seedling survival, or indirectly, by affecting seed predators.

Keywords

characterizing, recruitment, litter, postfire, environments, implications, seedling

Disciplines

Medicine and Health Sciences | Social and Behavioral Sciences

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CHARACTERIZING THE LITTER IN POSTFIRE ENVIRONMENTS: IMPLICATIONS FOR SEEDLING RECRUITMENT

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Litter accumulation after fire influences the magnitude of seed predation and seed germination. How litter accumulation and patchiness influence postfire seedling recruitment is poorly known. Species with persistent seed banks have seeds available for germination in the immediate postfire period. In contrast, plants with transient seed banks must flower after fire to place seeds in the postfire habitat. In southeastern Australian sclerophyll forests, most seedling recruitment occurs within 3 yr after fire. We found that less litter had accumulated in sites <6 mo postfire than in those 2–3 yr postfire. Seedlings of species with persistent seed banks therefore encounter postfire environments with large areas covered by little or no litter. Among these species there is great variation in seed mass, including some species with very light seeds. In contrast, the seed mass of transient seed bank species is less variable, with the lightest species more than 70 times heavier than the lightest persistent seed bank species. These seeds arrive 1–3 yr postfire and encounter habitats with more litter and fewer bare patches. This pattern suggests that litter accumulation after fire has influenced the evolution of seed mass either directly, by affecting germination and seedling survival, or indirectly, by affecting seed predators.

Keywords: fire, litter, seedling recruitment, seed size.

Introduction

Recruitment of seedlings into plant populations can be greatly affected by the amount and composition of the litter in which they occur (Fowler 1988; Facelli and Pickett 1991; Lamont et al. 1993; Jensen and Gutekunst 2003; Eckstein and Donath 2005). Litter appears to facilitate recruitment in some species but not others, depending on the size of seeds, their position in the litter, and their tolerance of shading and desiccation.

Litter can also influence the foraging activities of seed predators and their ability to locate seeds. Reduced amounts of litter after fire, for example, can improve the ability of vertebrate seed predators to locate seeds, thus increasing seed predation rates (Bond 1984; Clark et al. 1991; Myster and Pickett 1993; Auld and Denham 1999, 2001; Reed et al. 2006), despite any reduction in the population sizes of seed predators after fire (Fox 1982; Botha and Le Maitre 1992; Sutherland and Dickman 1999). Fire-induced modifications to the litter layer may influence the abundance, composition, and behavior of invertebrate seed predators and dispersers, particularly ants (Andersen 1988; Andrew et al. 2000; York 2000; Reed et al. 2004; Parr et al. 2007), with some species increasing in activity, resulting in variable levels of seed predation, depending on the characteristics of the habitat and the fire regime. However, predator satiation through the synchronous release of seeds after fire may nullify the impact of any increase in seed predation for plant species with canopy-stored seed banks (O'Dowd and Gill 1984; Wellington and Noble 1985; Bell et al. 1987; Andersen 1988; Lamont et al. 1991).

In fire-prone environments, considerable changes in the litter occur in relation to time since the last fire and its severity. In the first few days after fire, litter amounts are expected to be low and composed mainly of partially burned or unburned remnants of litter that was present before the fire. The amount of litter consumed will depend on the moisture content of the litter and other fuel components as well as the weather conditions at the time of the fire (McCaw et al. 1997). In the following weeks, many scorched leaves are expected to drop from the canopies of shrubs and trees, resulting in a rapid increase in the amount of litter (O'Connell et al. 1979; Andersen 1988; Birk and Bridges 1989; Burrows and Burrows 1992; Facelli and Kerrigan 1996). Subsequently, incremental or seasonal inputs are expected (Maggs and Pearson 1977) as the leaves of resprouting plants or seedlings senesce. Litter is also re-sorted over the landscape by wind and water, accumulating in some areas and leaving other patches bare (Lamont et al. 1993; Howell et al. 2006). The proportion of charcoal in the litter decreases as these components are incorporated into the humus (Raison et al. 1983) and as the overall amount of litter increases with new contributions through leaf fall. Equilibrium in the total amount of litter may occur when decomposition matches new contributions (Olson 1963; Hutson and Veitch 1985), although in many fire-prone ecosystems this is unlikely to happen before the next fire (Birk and Simpson 1980; Mitchell et al. 1986; but see Lamb 1985).

The changes in litter structure and amount immediately after fire have not been thoroughly studied. This is surprising,

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given that many characteristics of the postfire environment are strongly linked to the consumption of litter by fire. Surface insolation, soil moisture and heat flux, and wind and water erosion are greatly modified after fire (Whelan 1995; Auld and Bradstock 1996) and are all influenced by amount of litter cover. Most studies of litter dynamics relate to fire susceptibility, primary productivity, and ecosystem health for forest management (e.g., Conroy 1993; Duchesne and Wetzel 1999; McCaw et al. 2002). These studies often use traps suspended above the ground to estimate litter fall rates or combine litter with other components of fuel such as live plant tissues. They often do not sample the unconsumed litter after fire (but see McCaw et al. 1997; O'Connell and McCaw 1997) or account for the lateral movement of litter across the landscape. Similarly, although there has been much study of invertebrate populations after fire, few studies have carefully characterized the litter, the primary habitat of their target biota. A few studies have sampled in a manner that allows the assessment of the amount and composition of standing litter in relation to time since fire (Fox et al. 1979; O'Connell et al. 1979; Raison et al. 1983, 1986; Lamb 1985; Birk and Bridges 1989; Conroy 1993; York 1999), although spatial variation and early postfire measurements are not well sampled.

For plant species with germination and recruitment that is cued by fire, the amount of litter that germinating seeds encounter depends on when these seeds arrive in the environment. For species with persistent soil-stored seed banks, this depends only on how fire-related factors or postfire environmental conditions affect dormancy mechanisms or act to enhance germination, because the seeds are present in the soil before the fire. Most species that have persistent soil-stored seed banks recruit within a year of fire (Horton and Kraebel 1955; Purdie 1977; Keeley and Keeley 1981; Auld and Tozer 1995; Odion and Tyler 2002), although there are exceptions, such as those related to seasonal germination requirements (Roy and Sonie 1992; Ooi et al. 2004). Species that have canopy-stored seed banks vary in the timing of seed release, but generally their seeds fall within a year of a fire (Gill 1976; Bradstock and Myerscough 1981; Lamont and Barker 1988; Enright and Lamont 1989; Lamont et al. 1991), with recruitment occurring shortly after suitable rainfall events (Bradstock and O'Connell 1988; Benwell 1998). Hence, the seeds of species with either of these persistent seed bank types would usually encounter litter levels characteristic of recently burned sites. Species with transient seed banks include geophytic species that recruit soon after fire, with seedlings often seen 12–18 mo after fire (Le Maitre and Brown 1992; Tyler and Borchert 2002; Borchert 2004). These species resprout, grow rapidly, and flower soon after fire, often becoming inconspicuous after only 1 or 2 yr (Stone 1951; Keeley et al. 1981; Tyler and Borchert 2002). The seeds of some transient seed bank species are released into the habitat later still, that is, 12–36 mo after fire (Malanson and O'Leary 1982; Keeley and Keeley 1984; Auld 1986; Bradstock 1995; Benwell 1998; Curtis 1998; Taylor et al. 1998; Denham and Whelan 2000; Denham and Auld 2002), with germination dependent on rainfall events.

Independent of fire, seed mass has been found to be a good indicator of emergence and survival probability in relation to the amount of litter in which seeds germinate, with larger seeds more tolerant of litter (Seiwa and Kikuzawa 1996; Dzwonko and Gawronski 2002; Jensen and Gutekunst 2003; Moles and Westoby 2004; Eckstein and Donath 2005). Although it seems intuitive that seed predators would confound this relationship, since large seeds may be more valuable as a food source and more detectable than small seeds, Moles et al. (2003) found no evidence that, in general, larger seeds are more susceptible to predation.

In fire-prone sclerophyllous forests and shrublands most seedling recruitment occurs 0–3 yr after fire. During this postfire recruitment period, changes in the litter layer may influence the recruitment probabilities for plant species with different functional seed bank types. The litter may influence recruitment directly, by affecting germination and survival, or indirectly, by influencing the probability that seeds or seedlings are consumed by seed predators or herbivores. Based on the current understanding of litter accumulation after fire, we hypothesized that early in the postfire recruitment period (0–12 mo after fire), habitats would have low or highly variable amounts of litter, or both, and that later in the postfire recruitment period (>18 mo after fire), habitats would have a greater overall amount of litter more uniformly distributed. Following from this, we hypothesized that characteristics of the seeds of species with transient versus persistent seed banks may have been mediated by these changes that occur in the litter layer after fire.

The specific aims of this study were (1) to characterize the litter in the first 5 yr after fire by examining changes in the amount and variability in litter mass across a range of times that encompasses the postfire recruitment period for seedlings; (2) to examine the differences in seed mass among plant species from different functional seed bank types; and (3) to assess the interaction between timing of seed arrival and the amount of litter cover after fire to test the hypothesis that the evolution of seed mass has been influenced by postfire litter accumulation.

Methods

We sampled litter on two separate occasions (2005 and 2007). This allowed us to examine changes among replicate sites across the postfire seedling recruitment period (0–3 yr postfire) as well as changes after this recruitment period (4–5 yr). In 2005, we chose two replicate sites at each end of the seedling recruitment period: sites 1 and 2 (both <6 mo postfire) and sites 3 and 4 (2–3 yr postfire). In 2007, we repeated the sampling at each of these sites. This allowed us to make three planned comparisons: (1) the change in litter characteristics of two sites across the postfire recruitment period (sites 1 and 2 in 2005 vs. 2007), (2) the change in litter characteristics of two sites within the postfire recruitment period compared to beyond it (sites 3 and 4 in 2005 vs. 2007), and (3) the differences in litter characteristics of the two pairs of sites at the end of the postfire recruitment period (sites 3 and 4 in 2005 vs. sites 1 and 2 in 2007). This comparison tests whether site factors or time since fire has greater influence on litter characteristics.

The sites were located within 11 km of each other, between Colo Vale and Bargo in the southern tablelands of New South

Wales (lat. 34°23′S, long. 150°30′E). The vegetation at the sites varied from dry sclerophyll forest to woodland, but the sites had many plant species in common, including *Banksia serrata*, *Banksia spinulosa*, *Bossiaea obcordata*, *Corymbia gummifera*, *Cyathochaeta diandra*, *Entolasia stricta*, *Lomandra filiformis*, *Lomandra obliqua*, *Lomatia silaifolia*, *Patersonia glabrata*, *Persoonia levis*, *Pimelea linifolia*, *Platysace linearifolia*, and *Telopea speciosissima*. At each site, we set up

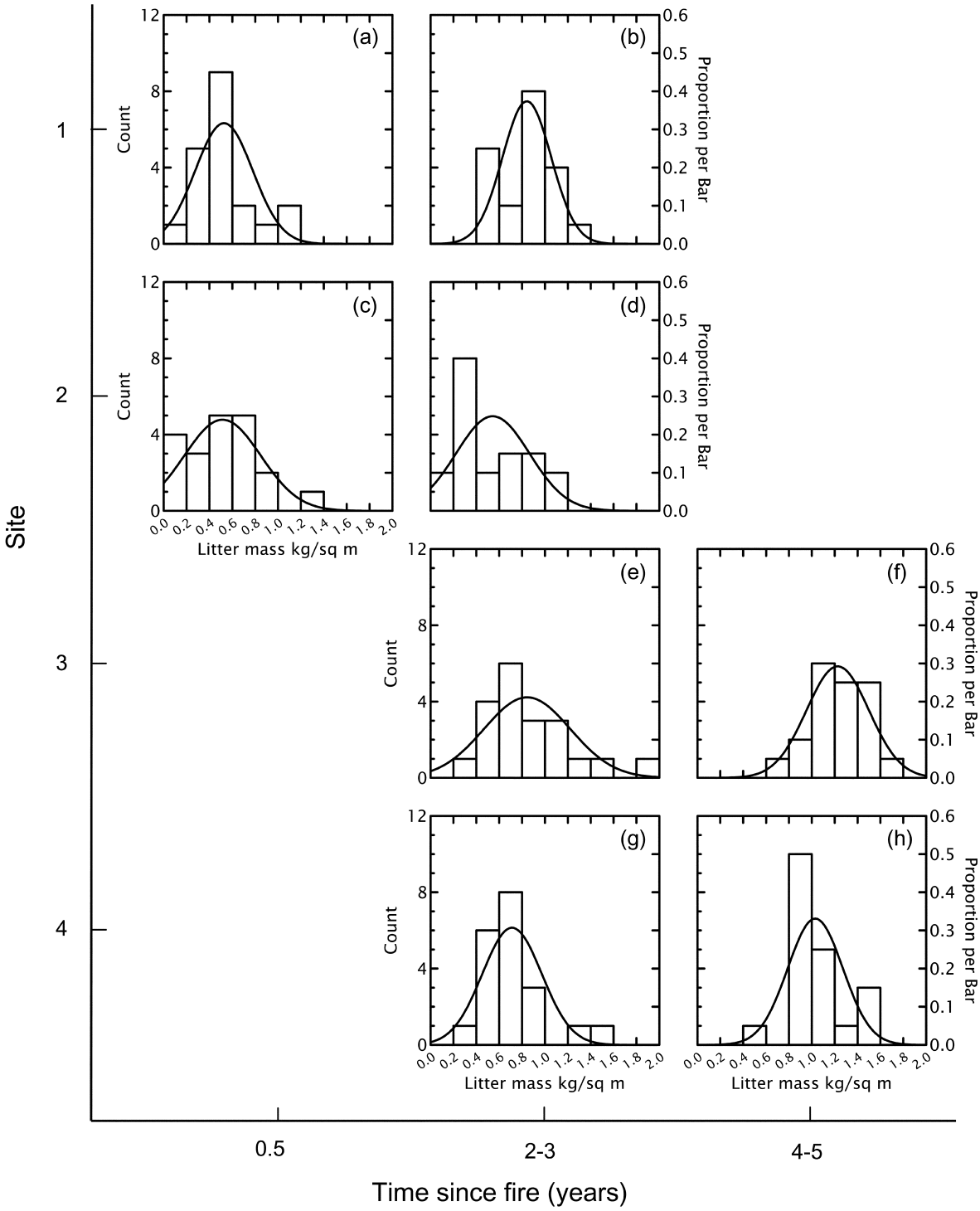

Fig. 1 Frequency histograms for the mass of litter (kg/m^2) for each site in 2005 and 2007. Plots are arranged to facilitate (1) comparisons of accumulation of litter from early to late in the postfire recruitment period (*a* and *c* vs. *b* and *d*), (2) comparisons of accumulation of litter from late in the postfire recruitment period into the postrecruitment period (*e* and *g* vs. *f* and *h*), and (3) comparisons among sites late in the postfire recruitment period (*b*, *d*, *e*, and *g*). The fitted line shows a normal curve with identical mean and variance as the data.

Table 1

Summary Statistics for Litter Mass at Each Site for Both Sampling Times

Site and sampling year	Time since fire (yr)	Mean litter mass (kg/m^2)	Variance	CV (%)
Site 1:				
2005	.5	.527 (.056)	.064	48
2007	2.5	.842 (.048)	.046	25
Site 2:				
2005	.5	.515 (.075)	.111	65
2007	2.5	.544 (.072)	.103	59
Site 3:				
2005	2	.844 (.085)	.143	45
2007	4	1.227 (.061)	.074	34
Site 4:				
2005	3	.712 (.058)	.067	37
2007	5	1.030 (.054)	.058	23

Note. Values in parentheses are standard errors. CV = coefficient of variation.

a 30 × 30-m (900-m^2) plot and marked 20 locations using randomly generated grid references. We placed a plastic cylinder (0.06 m^2, 5 cm tall) at each of these locations and harvested all litter from within it, cutting through leaves and sticks that were partially outside it.

The litter was weighed after being oven-dried at 80°C for 5 d. Litter mass in kg/m^2 was plotted using frequency distributions. Skewness (a measure of the symmetry of the distribution about its mean) and kurtosis (a measure of the length of the tail of the distribution) were calculated and were considered significant where the ratio of the measure to its standard error was greater than 2 (Wilkinson and Engelman 2005). Using an *F*-test, we compared the variances in litter mass, and using ANOVA, we compared the mean amounts of litter according to the three planned comparisons listed above.

To examine variation in seed mass in relation to timing of seed arrival after fire, we used data published by Westoby et al. (1990). From this data set of 332 species we extracted seed mass data for (i) species for which data on the functional seed bank type are available (transient seed bank, persistent soil, or canopy-stored seed bank); (ii) species known to be from fire-prone habitats (not rain forest and likely to burn more than once in 30 yr); and (iii) perennial shrubby species (or large perennial forbs such as *Xanthorrhoea* spp. and *Doryanthes excelsa*). We then compared the log (seed mass + 1) for species from different functional seed bank types to examine the variation and pattern of distribution of seed mass.

Results

Litter Sampling

Sites early in the postfire recruitment period had more samples with very little litter (falling into the first three columns of the graphs in fig. 1) than sites late in the postfire recruitment period. There was a wide range in the amount of litter from individual samples, from 0.035 kg/m^2 at site 2 in 2005 (fig. 1*c*) to 1.86 kg/m^2 at site 3 in 2005 (fig. 1*e*). Variance ranged from 0.046 at site 1 in 2007 to 0.143 at site 3 in 2005 (table 1). There was a reduction in variance over time at all sites. However, variance was not consistently greater at sites earlier in the postfire recruitment period (table 1), and there were no statistically significant results for *F*-tests in any of the planned comparisons (data not shown). Two sites at the end of the postfire recruitment period (sites 3 and 4 in 2005) had significant positive skewing, with site 4 in 2005 also showing positive kurtosis (fig. 1*e*, 1*g*). However, by these measures, in the 2007 sampling, the distributions at all of sites were not significantly different in shape from a normal distribution.

All comparisons supported the hypothesized trend of increasing litter mass with the passage of time after fire, although there were also significant site and site × time interactions in some comparisons (table 2). (1) The transition of sites 1 and 2 across the recruitment window (<6 mo–2.5 yr postfire). There was a significant increase in litter mass over the two sample periods, consistent with the notion of litter accumulation. However, there was also a significant site effect and site × time interaction resulting from a greater increase in litter mass at site 1 than at site 2 (table 2). (2) To estimate changes in litter accumulation and patchiness beyond the normal seedling recruitment window (sites 3 and 4 in 2005 vs. 2007), we tested whether the observed early accumulation of litter after fire continued beyond the period of postfire recruitment. The sites differed significantly from each other at each sample time, but both sites accumulated significant amounts of litter over time. (3) We compared sites from 2–3 yr postfire (sites 3 and 4 in 2005 vs. sites 1 and 2 in 2007). This comparison used data collected from different sites in different years to test how similar individual sites were at the end of the postfire recruitment window after different fires. One site (site 2) had significantly less litter than all the other sites, indicating that variation in fires, postfire conditions, and characteristics of the sites themselves may contribute to observed mass of accumulated litter at any one time after fire.

Table 2

Results of ANOVAs for Three Planned Comparisons of Litter Mass

Comparison and source	Sum of squares	df	Mean square	*F*	*P*
Accumulation .5–2 yr postfire:					
Site	.482	1	.482	5.957	.017
Time	.591	1	.591	7.305	.008
Site × time	.407	1	.407	5.032	.028
Error	6.154	76	.081		
Accumulation 2–5 yr postfire:					
Site	.538	1	.538	6.273	.014
Time	2.452	1	2.452	28.60	<.001
Site × time	.021	1	.021	.242	.624
Error	6.515	76	.086		
Site variation 2–3 yr postfire:					
Site (time)	1.062	2	.531	5.862	.004
Error	6.974	77	.091		

Note. Underlining indicates significant values.

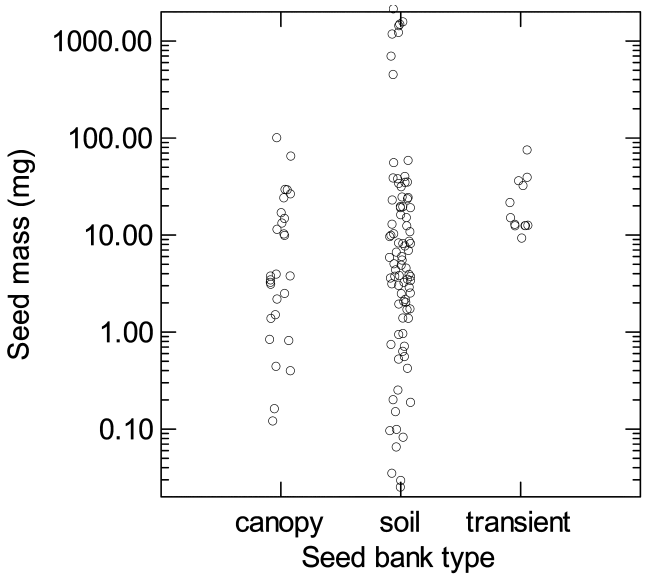

Fig. 2 Variation in seed mass among a selection of woody species from fire-prone areas in relation to seed bank type. Data are jittered for clarity; *Y*-axis is on a log scale. Canopy seed bank has 28 spp.; soil seed bank, 87 spp.; transient seed bank, 12 spp. Data are from Westoby et al. (1990).

Seed Mass Variation

Of the 332 species with seed mass published in the study by Westoby et al. (1990), some 187 were found to be from fire-prone habitats, with 127 of these considered shrubby perennial species with known seed bank types. This assessment was based on published information on plants of the Sydney region (Westoby et al. 1990; Benson and McDougall 1993, 1994, 1995, 1996, 1997, 1998, 1999, 2000, 2001, 2002, 2005) as well as data compiled by the New South Wales National Parks and Wildlife Service (NPWS 2002). Species were not evenly distributed among seed bank categories (canopy seed bank, 28 species; soil seed bank, 87 species; transient seed bank, 12 species), and neither were life forms, with large perennial forbs present only in the transient seed bank group. In addition, we omitted two transient seed bank species with very large seeds (*Macrozamia communis*, a cycad seed mass, 1841 mg; and *Livistona australis*, a palm seed mass, 2702 mg) from our analysis because they had no analogous representatives in either the soil or the canopy seed bank group. Soil-stored (coefficient of variation [CV] = 316%) and canopy-stored (CV = 153%) seed bank species showed great variability in seed mass, while species with transient seed banks were relatively constant in mass (CV = 76%; fig. 2). The minimum seed mass for species with transient seed banks (9.02 mg) was two orders of magnitude greater than that found for either soil- (0.029 mg) or canopy-stored (0.122 mg) seed bank species. Statistical comparisons among groups were greatly constrained by the relative paucity of species with transient seed banks. After transformation (log (seed mass + 1)) to reduce heteroscedasticity, mean mass of species with transient seed banks was not significantly different from the mean for either of the other two groups ($F_{2,124} = 2.04$, $P = 0.13$).

Discussion

There was a substantial increase in the amount of litter in habitats over the postfire seedling recruitment period. The litter was not consistently more variable in its distribution at the start of the postfire seedling recruitment period than at its end, and *F*-tests did not detect any significant change in variance. Our failure to statistically distinguish sites by their variance at particular times in the postfire recruitment period may result from the sensitivity of *F*-tests to deviations from normality (McGuinness 2002). Characteristics of nonnormality were apparent in our data, especially early in the postfire recruitment period. Visual examination of these data (fig. 1) allows an assessment of the degree of skewing and kurtosis, and in some samples this was statistically significant. The high degree of variability of the litter at some sites early in the postfire recruitment period probably results from the combination of patchiness in litter sources (mainly trees) and movement of fallen litter into patches by wind and water (fig. 3*A*), as observed by Lamont et al. (1993) and Howell et al. (2006). At the end of the postfire seedling recruitment

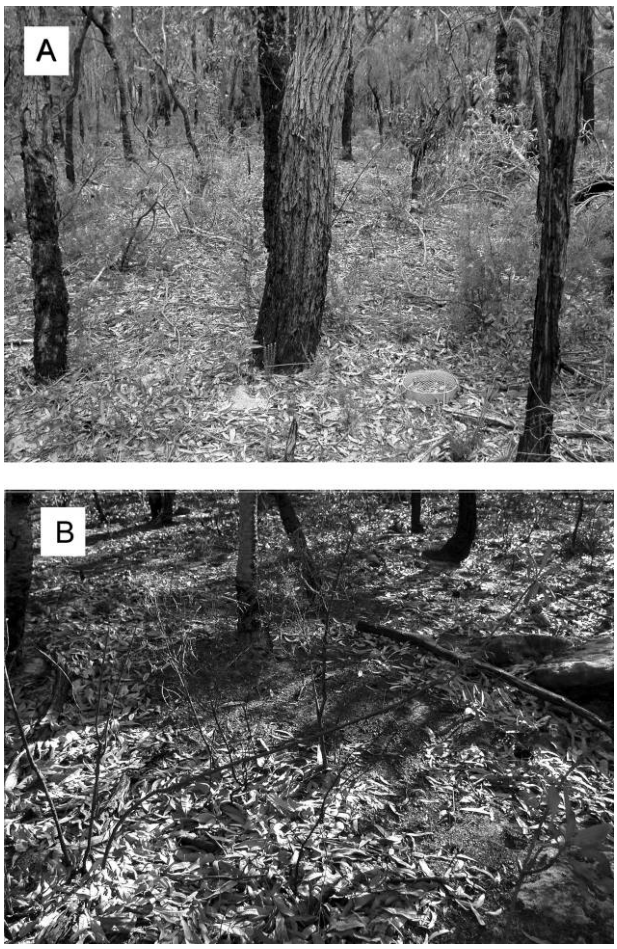

Fig. 3 *A*, Site 2, ~3 mo after fire, showing the accumulation of recently fallen scorched leaves into dense litter patches interspersed with areas of relatively bare ground. *B*, Site 3, ~2.5 yr after fire, showing a large amount of relatively homogeneously distributed litter.

period, the reductions we observed in variability may result from the creation or expansion of obstructions in the form of new or resprouting plants as well as from additional contributions of litter (fig. 3*B*). Expressing variance as CV provided evidence of reduced patchiness in litter in sites at the end of the postfire recruitment period (table 1). Overall, the range in CV across all sites (37%–65%) was comparable to values recorded by Whelan and York (1998) for sites 10 yr postfire (47%–68%), although those measurements included attached plant tissues.

As well as differences in the amount of litter at each end of the postfire recruitment period, there were significant differences among sites. The appearance and maintenance of such differences over time is likely to be due to a number of factors, including vegetation differences, microtopographic effects (such as the predominance of rock outcrops or variation in slope), differences in the most recent fire, and differences in fire history. Our observations suggest that the fire at site 2 was relatively intense, causing considerable canopy leaf scorch, while no canopy leaf scorch was apparent at site 1. It is more difficult to infer fire intensities 2 yr or more after fire, but survival of the stems of some individuals of lignotuberous species (*Petrophile pedunculata*) and fire-sensitive species (*Hakea sericea*) at site 3 suggest that this fire was of low intensity. This was not the case at site 4, where all stems of lignotuberous species and all fire-sensitive species were killed by the fire.

As a comparison with other studies of similar vegetation, the mean amount of litter at sites early in the postfire recruitment period (0.52 kg/m^2) in 2005 was close to that observed by Conroy (1993; 0.57 kg/m^2) but somewhat less than that observed by Hamilton et al. (1991). Birk and Bridges (1989) observed an increase in early postfire litter from 0.05 to 0.34 kg/m^2 in the first month as a result of the fall of scorched leaves, with a subsequent decline to 0.17 kg/m^2 after 12 mo. Our samples included the contribution of scorched leaves, but a decline in litter mass does not appear to have occurred, unless it was masked by a subsequent increase. The amount of litter found here for sites late in the postfire recruitment period (0.54–0.84 kg/m^2) fit well with values from other studies (e.g., Fox et al. 1979; Conroy 1993), although the higher values are greater than those reported by Conroy (1993). However, the time-since-fire categories employed by Conroy (1993) overlap at 3 yr, with a rapid increase in litter mass between 1 and 3 yr (0.64 kg/m^2) and between 3 and 6 yr (1.14 kg/m^2) since fire, suggesting that data presented here are likely to fit between these two categories. Measurements of litter mass in 2007 for sites with more time since fire (4–5 yr postfire in 2007) match well with Conroy's estimations.

Although we found only weak support for a decline in variance of litter mass over the postfire recruitment period, evidence for an overall increase in litter mass supports our prediction that the availability of litter-free space decreases with increasing time since fire. The implications of this trend for postfire plant recruitment vary depending on the timing of seed arrival after fire. Seeds of canopy seed bank species arrive soon after fire and will fall into a habitat that has a relatively small amount of litter overall as well as some areas with little or no litter. If the release of seeds occurs before or soon after the fall of scorched leaves from the canopy, these seeds are likely to be moved along the surface by wind and water (Hammill et al. 1998), possibly into dense litter drifts or litter dams (Lamont et al. 1993; Howell et al. 2006). If release occurs some time after the fall of scorched leaves, the seeds may remain where they fall, with their destination independent of the litter distribution. In these scenarios, seeds fall into a patchy litter environment and are exposed to variable edaphic conditions and probability of predation. Similarly, seedlings from soil seed bank species will encounter varying litter amounts when they emerge in the first postfire year. Thus, conflicting selective pressures may prevent the development of specialization in seed characteristics. Alternatively, the broad range of conditions that may be experienced by seeds within the soil or released from fruits in the canopy may allow a large range of seed sizes to persist, with some specializing in recruiting in more mesic microsites (smaller seeds) and others in more xeric sites (larger seeds), as observed by Milberg and Lamont (1997) and Lamont and Groom (2002). In contrast, seeds of shrubby species with transient seed banks are released up to 3 yr after fire (Denham and Auld 2002). Seeds of these species fall after a considerable amount of litter has accumulated in the habitat, mostly into areas with higher levels of litter cover than the areas of other seed bank types. Unless they fall into the rare patches with little or no litter, seeds may need particular characteristics that would enable them to germinate and establish in litter. Furthermore, if their seeds do fall into patches with little or no litter, they will be more susceptible to predation from populations of seed predators that have by then reestablished (Fox 1982).

The selective pressures resulting from these different influences of seed predators and different physical attributes of habitats may have led to more specialized seed characteristics. It is generally accepted that greater shade tolerance and ability to emerge from under litter is found in species with high seed mass (Seiwa and Kikuzawa 1996; Reich et al. 2003; Moles and Westoby 2004). Our selection from Westoby et al. (1990) of woody species in fire-prone areas in the Sydney Basin showed a high degree of variation in seed mass for soil and canopy seed bank species, encompassing very small to very large seeds (fig. 2). In contrast, the transient seed bank species showed limited variation, with minimum seed mass much greater than that of the other groups (fig. 2). The reduced variation in seed mass among these species provides support for the notion that selective pressures may have led to this seed size characteristic. The much greater minimum seed mass suggests that there may be a threshold seed mass below which successful recruitment in this group of species would be minimal. Further exploration of potential seed characteristics or selective forces should be made through experimental manipulations of predator access, litter amount, and timing of seed release with time since fire among species with different modes of postfire regeneration.

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